

## Chapter 4

**THE EFFECTS OF UNDERSTORY VEGETATION AND FOREST  
MANAGEMENT ON FOOD RESOURCES FOR SONGBIRDS IN WESTERN  
OREGON**

## INTRODUCTION

The correlations of songbird abundance and diversity with structural or compositional attributes of habitats has been studied by avian ecologists for decades (MacArthur and Mac Arthur 1961, Karr and Roth 1971, Willson 1974, Wiens and Rotenberry 1981, Verner et al., 1986 Block and Brennan 1993), although mechanisms underlying such relationships are seldom studied and not well understood. Such correlational relationships have guided methods of habitat assessment and management (e.g., USF&W Habitat Evaluation Procedures), which tend to rely mainly on quantification of vegetation characteristics thought to be related to species' life requisites, rather than on measurements of the ultimate resources provided by the vegetation (i.e., food and cover). However, few empirical data are available to validate assumptions regarding the basis for relationships between vegetation and resource requirements of birds. This lack of information represents an obstacle for managers concerned with providing quality habitat for songbirds.

One factor that is likely to drive habitat relationships for any wildlife species is food. Food availability is a basic, critical habitat component that often limits the reproductive success and survival of breeding birds (Martin 1987). Distribution and abundance of food has been correlated with population size of birds and is a major factor in habitat selection (Wiens 1989, Gill 1994: 512 – 516). Food resources for forest birds may be directly or indirectly associated with vegetation. Seeds, fruits, and flowers provide a direct source of food for many bird species, while arthropod prey that live on plants indirectly link avian insectivores to vegetation. Although food availability is typically difficult to measure, an understanding of the trophic pathways from vegetation

to songbirds would provide an empirical foundation for the management of vegetation to achieve objectives aimed at providing habitat for birds.

The first step in understanding trophic links between birds and vegetation is to determine the composition of birds' diets. Once the composition of the diet is known for a bird species, it should be possible to identify the plant species and or habitat conditions that are important in supporting those food resources. Because each bird species has a unique diet, food availability must be measured separately for each species (Holmes and Schultz 1988). Unfortunately, even basic information on the composition of diets is lacking for most avian species. Some authors have sidestepped this lack of information by assuming that abundance of actual prey is correlated with estimates of overall arthropod abundance (Hutto 1980, Hutto 1981b, Blake and Hoppes 1986). This method has been used successfully to predict bird density at the community level (Brush and Stiles 1986), but because many species are at least somewhat selective, this approach may not accurately represent food availability for individual species.

Although there is little detailed knowledge of bird diets (especially for birds that breed in Pacific Northwest forests), we know, in general, that arthropods that dwell on vegetation constitute an important portion of the diet of many forest bird species (Erich et al. 1988, Marcot and Vander Heyden 2001). Because most forest insects use specific host plant species (Edwards and Wratten 1980), each plant species supports a characteristic assemblage of herbivorous insects. Both diversity and abundance of herbivores vary among plant species (Schowalter 2000). Herbivorous insects in turn can have associated arthropod predators and parasites, which also may be prey for birds. Therefore, although most bird species may not be directly associated with particular plant species, they may be linked to certain plant taxa through their insect prey (Holmes and Robinson 1981). Furthermore, some plant species provide direct food resources for birds in the form of seeds and fruits.

Understory plant species contribute a major proportion of the floristic diversity in Pacific Northwest conifer forests (Halpern and Spies 1995) and may therefore be presumed to be important in supporting faunistic diversity. However, little is known about arthropod assemblages on understory plants, particularly which plant species may

be most important in supporting the arthropods that are prey for birds. In this chapter, I present basic information on dietary composition and distribution of food resources for several species of songbirds that commonly breed in forests of the Pacific Northwest. I chose to focus this investigation on birds associated with understory vegetation because of the important contribution to diversity made by the understory, and its accessibility for sampling birds and arthropods. Ultimately, I wanted to know how structure, composition, and management of understory vegetation influence food availability for songbirds that primarily forage in the forest understory.

## METHODS

### Study Sites

All study sites were located in the Western Hemlock Vegetation (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1988) of the Oregon Coast Range. Mild, wet winters and dry summers characterize regional climate. Sites comprised lands managed by three public agencies (Bureau of Land Management, U.S. Forest Service, Oregon State University).

In order to link my results to a larger ecological framework, and build upon existing data, I sampled songbird diets and arthropod populations in a subset of study sites used in an integrated study that assessed differences in the diversity of various organisms among young unthinned, young thinned, and old-growth Douglas-fir stands in western Oregon (Muir et al. 2002). I used three triads of stands in the Oregon Coast Range, each consisting of a geographically grouped set of one young unthinned, one young thinned, and one unmanaged, mature stand (Sand Creek, Mary's Peak, and D-line Road (Fig. 2.1); Muir et al. 2002). The young stands (thinned and unthinned) regenerated naturally following clear-cut harvesting and were 55 – 75 years old. One age cohort dominated the overstory, with very few large trees and well decayed snags (<1/ ha) persisting from previous stands. Unthinned stands were in stem-exclusion stage of forest development (Oliver and Larson 1990), and were characterized by a dense,

uniform overstory of Douglas-fir, and a sparse understory. Thinned stands had been thinned to uniform spacing 19 – 28 years prior to this study. Mature stands of the triads had vegetation and structure typical of old-growth, as described by Spies and Franklin (1991). The stands I sampled were chosen to represent a range of variability in understory structure and to maximize captures of birds associated with forest understory. I added two pairs of stands not used in the study described by Muir et al. (2002) to increase the number of fecal samples collected from focal bird species. These sites were located in McDonald-Dunn State Forest, and consisted of two unmanaged, mature (120 years old) stands, each paired with a stand of the same age that had been partially harvested with a group selection method. A study by Chambers (1996) indicated a high abundance of shrub-associated bird species in these stands. Characteristics of overstory tree density and understory vegetation cover for the McDonald-Dunn State Forest sites are described in Chapter 2. All stands were located in the Western Hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1988) between 200 and 500 m elevation.

#### Field and Lab Methods

Mist-nets were used to capture birds for the purpose of collecting fecal samples. Eight to 10 nets were operated on two to three dates in each stand between mid-May and mid-July 1996, 1997, 1999 and 2000. Nets were 12 m in length, and were set to intercept birds moving between 0.3 to 2.5 m above ground. Within the boundaries of each stand, nets were placed opportunistically where vegetation provided sufficient screening to camouflage the mesh, and where bird activity was believed to be high. Nets were opened within ½ hour of sunrise, and remained in operation for  $\geq 4$  hours, or until rain or wind forced closing. Birds were held in a cloth bag for up to 45 minutes or until they defecated. Fecal samples were collected in glass vials and stored in 70% ethanol pending identification of contents.

I examined 87 fecal samples collected from Wilson's warblers in 1996 and 1997 and 96 samples from Swainson's thrushes in 1996, 1997, 1999, and 2000 under a binocular dissecting microscope. I identified fragments to the lowest taxonomic level

possible, using well-illustrated entomology texts and guides (Borror and White 1970, Shattuck 1985, Moldenke et al. 1987, Borror et al. 1989) and expert opinion (Andrew Moldenke, Oregon State University; Greg Brenner, Pacific Analytics Inc., Albany, OR). Recognizable pieces from each sample were mounted on glass slides. I estimated the number of individuals within each taxon in a fecal sample by summing head capsules, pairs of mandibles, or sets of legs that were similar in size and color. Mandibles could usually be identified as originating from either the right or left side of a head capsule, so two mandibles from the same side could be inferred as representing two individuals. I measured length of whole femurs, tibiae, mandibles, and head capsules using an ocular micrometer fitted on the microscope.

To estimate the length of arthropod prey from fragments, I developed regression equations quantifying relationship of whole body length to leg fragments for 11 taxonomic groups of adult arthropods and to mandible length for larvae (Table 4.1). I measured femur, tibia, and whole body lengths of adult arthropods ( $n=175$ ), and mandible and body lengths of larvae ( $n=21$ ) collected from understory vegetation (see below). I estimated original sizes of items eaten by birds by applying regressions to whole tibiae, femurs, and mandibles in fecal samples. For spiders, I averaged predicted body lengths derived from femora and tibiae because I was unable to distinguish femurs from tibiae in fecal samples.

I examined 139 fecal samples collected from Swainson's thrushes, and 27 samples collected from seven additional species in 1997, 1999, and 2000 for presence of seeds. Seeds from each sample were counted and identified. Reference seeds were collected from fruits simultaneously with collection of fecal samples in order to aid in identification of the plant of origin to genus or species. The proportion of fecal samples containing seeds was calculated for each plant species. I calculated the proportion of Swainson's thrush fecal samples with seeds for six 10-day periods between 21 May and 22 July.

Table 4.1. Regression equations used to reconstruct original sizes of prey items from fragments in fecal samples of songbirds, Oregon Coast Range.

Arthropod	N	Length Range <sup>1</sup> (mm)	Regression Equations	R <sup>2</sup>
Insects <sup>2</sup>	175	1.2 – 12.5	$\ln(\text{body}) = 1.412 + 0.841 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.379 + 0.738 * \ln(\text{tibia length})$	0.58 0.48
Coleoptera	79	2.1 – 12.5	$\ln(\text{body}) = 1.612 + 0.808 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.645 + 0.794 * \ln(\text{tibia length})$	0.65 0.74
Cantharidae	20	2.5 – 9.3	$\ln(\text{body}) = 1.721 + 1.039 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.701 + 1.033 * \ln(\text{tibia length})$	0.81 0.78
Curculionidae	10	3.1 – 9.6	$\ln(\text{body}) = 1.315 + 0.929 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.437 + 0.853 * \ln(\text{tibia length})$	0.92 0.91
Mordellidae	10	2.7 – 4.6	$\ln(\text{body}) = 1.657 + 1.166 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.660 + 0.776 * \ln(\text{tibia length})$	0.91 0.91
Diptera	57	1.2 – 12.0	$\ln(\text{body}) = 1.134 + 0.843 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.114 + 0.886 * \ln(\text{tibia length})$	0.75 0.77
Hymenoptera (winged adults)	12	1.2 – 11.0	$\ln(\text{body}) = 1.428 + 0.936 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.467 + 1.007 * \ln(\text{tibia length})$	0.79 0.81
Formicidae	6	2.8 – 9.0	$\ln(\text{body}) = 1.387 + 0.773 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.486 + 0.786 * \ln(\text{tibia length})$ $\ln(\text{body}) = 0.894 + 0.780 * \ln(\text{leg length})$	0.99 0.98 0.99
Homoptera / Hemiptera <sup>3</sup>	10	1.8 – 11.2	$\ln(\text{body}) = 1.609 + 1.193 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.444 + 0.864 * \ln(\text{tibia length})$	0.48 0.25
Aphididae	6	2.2 – 3.1	$\ln(\text{body}) = 0.932 + 0.372 * \ln(\text{femur length})$	0.35
Larvae <sup>4</sup>	21	6.5 – 26.0	$\ln(\text{body}) = 3.633 + 0.890 * \ln(\text{mandible length})$	0.64
Spiders	19	0.8 – 6.0	$\ln(\text{body}) = 0.956 + 0.078 * \ln(\text{femur length})$ $\ln(\text{body}) = 1.125 + 0.590 * \ln(\text{tibia length})$	0.63 0.65

<sup>1</sup> Minimum and maximum body lengths (frons to tip of abdomen) of specimens measured for regression equations.

<sup>2</sup> Adults of all orders except spiders. Equation used for unidentified prey items.

<sup>3</sup> Excluding aphids.

<sup>4</sup> Includes Lepidoptera and Hymenoptera (sawfly) larvae

### Collection of Arthropod Samples

Arthropods were collected from understory vegetation in the same stands where fecal samples were collected and within 10 days of each mist-netting session in each stand in order to coincide spatially and temporally with collection of fecal samples from birds. A shrub-beating method (Borrer et al. 1989, Cooper and Whitmore 1990) was used to sample sedentary arthropods that are potential prey for foliage-gleaning

songbirds on vegetation <2 m above forest floor. In 1996 and 1997, arthropods (and fecal samples) were collected from most sites during two periods each year: first between 26 May and 26 June, and again between 30 June and 30 July. In 1999 sampling took place during one period in each stand, between 27 May and 17 June.

Woody shrubs and/or ferns at 50- to 75-m intervals along randomly established transects in each stand were selected for sampling. Species of vegetation sampled varied within and between stands because the two most dominant (by cover) woody shrub and/or fern species at each sampling point were selected for beating. In each sampling period, 8 – 31 beating samples from each stand were collected. A different transect was established in each stand for each sample period within a year. One sample of a shrub was approximately equal to 100 leaves (vine maple, ocean spray, and salmonberry), 50 leaves (salal and hazel), 5 fronds of bracken fern and 8 of sword fern, or 1-m<sup>2</sup> branch (western hemlock). Arthropods were dislodged from branches and foliage onto a 1-m<sup>2</sup> canvas sheet and aspirated into vials. The foliage sampled was collected, dried, and weighed, and the arthropod specimens were preserved in 70% ethanol. Some shrub samples spoiled prior to weighing, resulting in missing data. Weights of unspoiled samples of the same species were averaged to derive an estimate of weights for missing measurements.

### Data Analysis

I calculated the frequency of occurrence of arthropod groups in the diets of Hammond's and Pacific-slope flycatchers, Swainson's thrushes, Wilson's warblers and MacGillivray's warblers. Frequency of occurrence in the diet was calculated as the number of fecal samples containing a given arthropod group divided by the total number of fecal samples. The lowest taxonomic levels that could be identified from fragments in fecal samples defined arthropod groups used for analyses. To derive a measure of prey available for Wilson's warblers, I calculated frequency of occurrence of arthropod groups from all beating samples (all shrub species pooled) collected in 1996 and 1997, the same years for which I had Wilson's warbler diet data. I compared the frequency of occurrence of arthropod groups in the diet of Wilson's warblers with

frequency of occurrence on shrubs, and ranked groups by the ratio of frequency of occurrence in diet to that on shrubs. I used this forage ratio (Krebs 1989) as an index of prey selection by Wilson's warblers, with ratios  $>1$  indicating greater than expected use based on availability *in the understory* (see Discussion for explanation of limitations of this approach). I focused analyses of prey sizes and comparisons of prey availability among plant species and shrub conditions on arthropod groups that occurred in  $>60\%$  of Wilson's warbler diets and had forage ratios  $>1$ . I did not compare frequency of occurrence of arthropod groups in diets and on shrubs for other bird species because I did not believe beating samples adequately represented potential food for Swainson's thrushes (they frequently foraged on the ground; see Chapter 3), and because sample sizes were too small for the other three species.

I used the Kolmogorov-Smirnov statistic to test whether the distribution of arthropod sizes was the same for arthropods consumed by Wilson's warblers as for arthropods collected from vegetation (Steel and Torrie 1980). I used this method to compare size distributions for arthropod groups: larvae (including Lepidoptera and Symphyta (sawflies)), Diptera, Coleoptera, and Homoptera, and all adult arthropods pooled. I used an alpha level of 0.05 to determine a significant difference.

I calculated two indices of arthropod intensity: abundance and biomass. Intensity is a measure of the arthropod load per unit of plant material. Arthropod weights were calculated from regression models (Appendix A). To calculate average abundance and biomass intensity for each stand condition, I summed the total number of individuals and the total weight of all individuals in each category over all plant samples within a stand in each sample period in each year and divided by the corresponding total dry weight of plant material. These indices were averaged across stands within each condition, period, and year to derive stand condition means and 90% confidence limits. To calculate average abundance and biomass intensity on each plant species, I summed the total number of individual arthropods and the total weight of all individuals in each category over all samples of each plant species within a stand in each sample period in each year and divided by the corresponding total dry weight of



plant material. These indices were averaged across all stands within each period and year in which each plant species was sampled.

I compared the intensity of four arthropod categories (adult Coleptera and Diptera >3 mm, larval Lepidoptera >6 mm in length, and all arthropod prey combined) among plant species and stand conditions using analysis of variance (ANOVA). I included sawfly larvae with the Lepidoptera larvae group because they are similar in form and also had a forage ratio >1. The combined category of arthropod prey included Coleptera and Diptera >3 mm, Lepidoptera and Symphyta larvae >6 mm, and all other arthropods >2 mm in length (except Diplopods), based on taxa and sizes of prey consumed by Wilson's warblers and other bird species.

I tested for the effects of plant species and stand condition separately because not all plant species occurred in all stand conditions. For all responses, except Lepidoptera intensity, I used ANOVA to test the null hypothesis of no difference in arthropod intensity among seven plant species that were sampled in  $\geq 3$  stands in  $\geq 2$  years. All data met assumptions of normal distribution and constant variance for ANOVA after log-transformations. I used the non-parametric Kruskal-Wallis test for comparing intensity of Lepidoptera larvae among plant species and stand conditions because the distribution of response values that resulted from a high proportion of samples with no larvae could not be corrected with a transformation. Because this was an exploratory analysis and I did not want to overlook possible biologically significant relationships, I used  $\alpha = 0.10$  to evaluate significance of effects. For tests of plant species effects with  $P < 0.10$ , I evaluated overlap of 90% confidence intervals to compare responses between each pair of plant species (Steidl et al. 1997). I tested for an overall effect of stand condition on the response variables with all plant species pooled within each stand condition. I also tested for an effect of stand condition separately for plant species that were sampled  $\geq 3$  times in  $\geq 2$  conditions (vine maple, salal, oceanspray, and sword fern). Group selection stands were not included because the sample size was too small ( $N=2$ ). For tests of stand condition effects with  $P < 0.10$ , I evaluated overlap of 90% confidence intervals to compare responses between each pair of plant species.

The abundance and biomass intensity indices described above estimated arthropod prey loads per unit of plant material. Because prey load varied with plant species, and cover of each plant species varied among stands, I also calculated cover-weighted indices that would reflect abundance and biomass of arthropod prey at the stand level. To derive these indices, I summed abundance and biomass of all arthropods >2 mm in length, except taxa that were never found in bird diets, for each plant species sampled in each stand in each year and divided by the total dry weight of each plant species. I multiplied these indices by a standardized estimate of cover for each plant species sampled to derive the final cover-weighted indices for each stand. I used shrub cover data from line transect estimates (see Chapter 2) and unpublished data for the Sand Creek sites (not sampled in 1999 and therefore not included in Chapter 2). I averaged cover-weighted abundance and biomass indices over years, log-transformed both indices to meet model assumptions, and compared among thinned, unthinned, and mature stand conditions using ANOVA and 90% confidence intervals. I did not include the GS stands and their paired mature stands in this comparison because those data were limited to one year.

## RESULTS

### Arthropod Prey of Wilson's warblers

More than 10 orders of arthropods were found in 87 Wilson's warbler fecal samples from 1996 and 1997 (Table 4.2). I was able to identify few arthropod fragments from fecal samples to below the taxonomic level of order. Families identified were Homoptera: Achilidae, Aphididae and Cercopidae; Neuroptera: Chrysopidae; Coleoptera: Cantharidae and Mordellidae; Diptera: Empididae, Mycetophilidae and Sciaridae.

Lepidoptera larvae, Homoptera, Diptera, and Coleoptera had high frequencies of occurrence in fecal samples (>60%), and had forage ratios >1 (Table 4.2). Adult Lepidoptera and arthropod eggs had the highest forage ratios, but occurred relatively

infrequently in the diet and were extremely rare on shrubs. In contrast, spiders occurred frequently in the diet, but were very common on vegetation.

Table 4.2. Percent occurrence of arthropods in diets of Wilson's warblers (n=87) and on shrubs (n=681 samples from beating), 1996-1997, Oregon Coast Range. The ratio of the frequency of occurrence in diet to that on shrubs (forage ratio) is interpreted as an index of prey selection, with ratios >1 indicating greater than expected use based on availability.

Arthropod Taxa	% Occurrence in Diet	% Occurrence on Shrubs	Forage Ratio
Lepidoptera, adults	0.18	<0.01	45.98
Unknown arthropod eggs	0.14	0.01	11.49
Lepidoptera, larvae *	0.63	0.12	5.06
Homoptera (all taxa) *	0.86	0.51	1.69
Diptera *	0.99	0.59	1.67
Hymenoptera, wasps	0.46	0.28	1.67
Hymenoptera, Symphyta larvae	0.20	0.12	1.64
Coleoptera (all taxa) *	0.84	0.58	1.45
Homoptera, Cercopidae	0.23	0.16	1.44
Araneida (all spiders)	0.85	0.90	0.94
Neuroptera	0.05	0.07	0.67
Acari (mites)	0.02	0.20	0.11
Collembola	0.05	0.56	0.08
Psocoptera	0.02	0.31	0.07
Hemiptera	0.01	0.19	0.06

\* Groups selected for comparison of abundance and biomass intensity among shrub species and stand conditions

Sizes of adult arthropods consumed by Wilson's warblers averaged approximately 4 mm (Table 4.3), and ranged from 2 to 10 mm (Fig. 4.1A). The size distribution of adult arthropods consumed was significantly different than the distribution for available adult arthropods (Kolmogorov-Smirnov two-sample test,  $P < 0.0001$ ), indicating that Wilson's warblers consumed prey that were larger than the most abundant items available. This pattern was consistently significant across the most

frequently consumed arthropod groups (Fig. 4.1A - E). However, I did not find evidence of the largest size classes (>12 mm) of adult arthropods, including flies, beetles, and spiders, in the diet.

Larvae, primarily sawflies (Hymenoptera: Symphyta) and Lepidoptera, were the largest prey items consumed by Wilson's warblers. Larvae ranged from approximately 6 – 26 mm in length. As with adult arthropods, the size distribution of larvae consumed was significantly different than that of available larvae (Fig. 4.1E) because warblers were eating mostly the larger (>6 mm) larvae that occurred less frequently than those in the smaller size classes.

Table 4.3. Average lengths (mm), with confidence intervals, and ranges of arthropods in Wilson's warbler diet (1996, 1997) estimated from regressions of arthropod body length on leg length or mandible width. Confidence intervals not calculated for taxa with <10 size estimates.

Arthropod Taxa	N <sup>1</sup>	Mean	95% CI	Range
Adult Arthropods	559	4.1	3.92, 4.18	0.9 – 9.8
Coleoptera	134	4.7	4.44, 4.98	2.2 – 9.1
Cantharidae	4	5.0	---	3.2 – 6.5
Mordellidae	3	3.7	---	3.0 – 5.0
Diptera	230	3.6	3.46, 3.85	1.4 – 9.8
Hymenoptera (adults)	53	4.2	3.81, 4.62	2.2 – 8.9
Homoptera (incl. Aphids)	33	5.7	5.06, 6.39	1.2 – 9.5
Aphids	9	4.3	3.73, 4.91	3.3 – 5.5
Larvae				
Lepidoptera	77	13.7	12.73, 14.62	5.9 – 25.8
Sawfly	19	14.9	12.97, 16.88	9.9 – 25.0
Collembola	5	1.5	---	0.9 – 1.8
Spiders	73	3.4	3.34, 3.52	2.6 – 4.5
Unknown Egg	7	0.6	---	0.6

<sup>1</sup> Number of individual arthropods in fecal samples from both years combined used to estimate size of items in diet.

Figure 4.1. Distribution among size classes of A) adult arthropods, B) Coleoptera, C) Diptera, D) sawfly and lepidoptera larvae, and E) Homoptera available as prey and those consumed by Wilson's warblers in the Oregon Coast Range, 1996 and 1997.

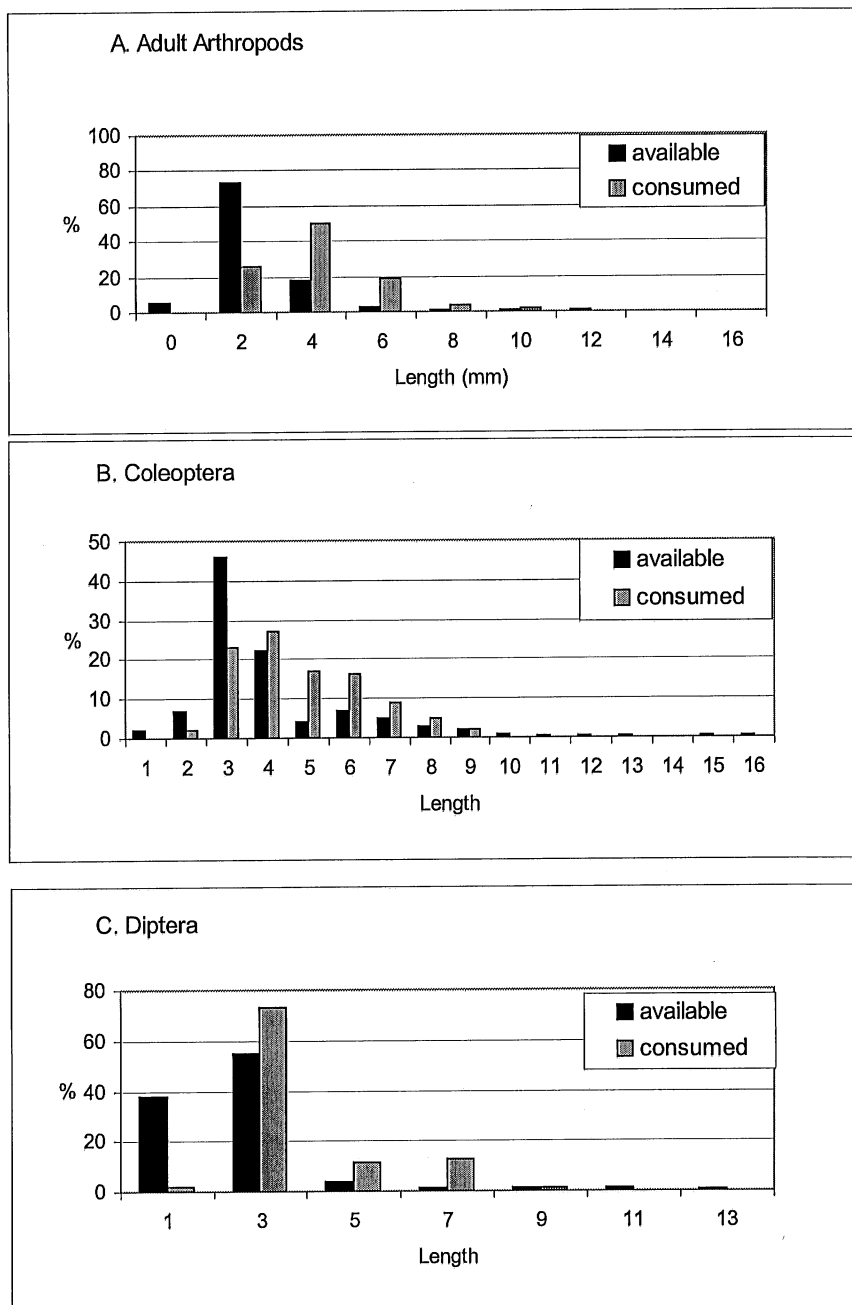
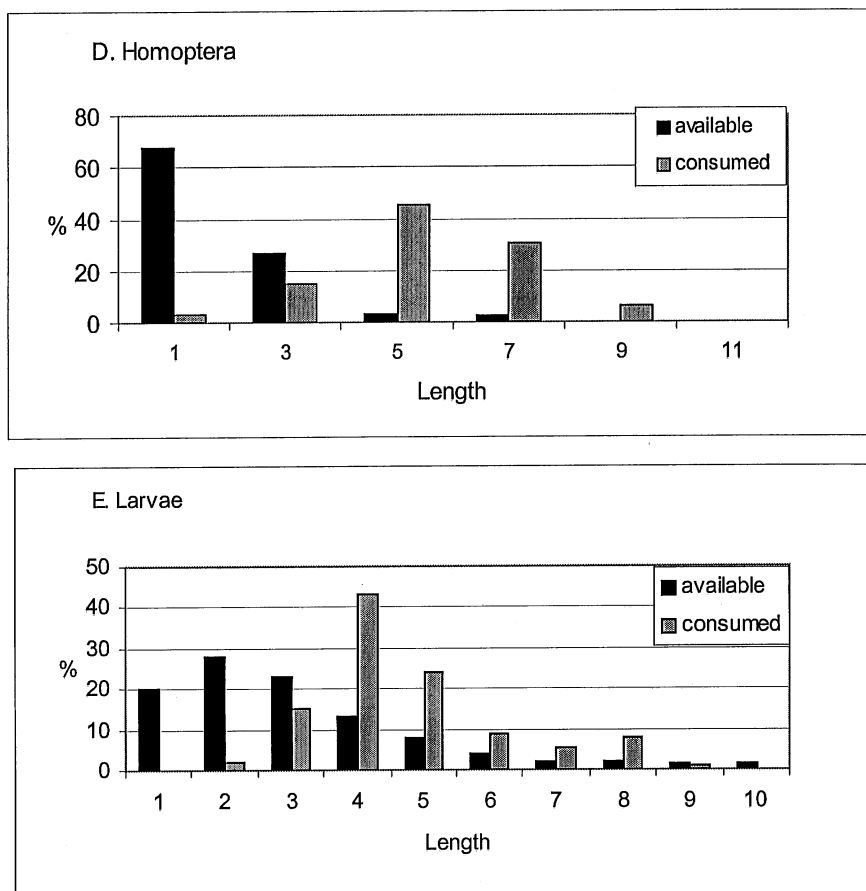


Fig. 4.1. Continued.



### Arthropod Prey of Swainson's Thrushes

Twelve orders of arthropods were identified from fragments in 96 fecal samples collected from Swainson's thrushes during four years (1996, 1997, 1999, 2000; Table 4.4). Beetles and ants were the predominant prey items, occurring in >70% of the fecal samples. Of the 12 families of beetles identified from fragments, weevils (*Curculionidae*) occurred the most frequently. Swainson's thrushes also frequently consumed spiders and flies (each found in approximately 50% of fecal samples).

Sizes of arthropod prey consumed by Swainson's thrushes ranged from 1 – 30 mm, with an overall average of 6.95 mm (Fig. 4.2). Ninety-three percent of the prey items were  $\geq 3$  mm in length. The largest taxa consumed were Hymenoptera (sawfly) and Lepidoptera larvae (Table 4.4).

Table 4.4. Percent frequency of occurrence (proportion of total number of samples) and sizes of arthropod prey in 96 Swainson's thrush fecal samples from four years. Orders include all families identified; families identified in  $\geq 3$  samples also are listed independently.

Arthropod Taxon	%	Prey Size (mm)			N <sup>1</sup>
		Average (SE)	Min	Max	
Coleoptera <sup>2</sup>	91	7.92 (0.22)	2.06	16.72	146
Curculionidae	26	7.16 (0.49)	4.56	11.31	15
Scolytidae	3	-	-	-	-
Hymenoptera <sup>3</sup>	77	5.75 (0.26)	2.68	24.90	131
Formicidae	75	5.43 (0.19)	2.68	12.00	124
Tenthredinidae (larvae)	11	19.92 (2.52)	16.73	24.90	3
Arachnida	54	3.64 (0.25)	2.60	4.55	8
Diptera	51	5.53 (0.57)	1.88	22.00	36
Tipulidae	6	5.32 (---)	-	-	1
Lepidoptera (larvae) <sup>4</sup>	43	18.01 (1.28)	11.01	29.28	21
Homoptera	9	6.16 (0.95)	4.51	7.81	3
Cercopidae	4	6.16	-	-	1
Neuroptera	3	-	-	-	-
Collembola (Entomobryidae)	2	2.16 (0.53)	1.63	2.69	2
Hemiptera (Miridae)	2	-	-	-	-
Microcoryphia (Machilidae)	2	-	-	-	-
Orthoptera	2	6.37	-	-	1
Apterygota	1	-	-	-	-

<sup>1</sup> N is the number of fragments in fecal samples used to estimate prey size (length of body from frons to the posterior tip of the abdomen).

<sup>2</sup> Includes Buprestidae, Cantharidae, Carabidae, Cincindelidae, Coccinellidae, Curculionidae, Elateridae, Mordellidae, Scarabidae, Scolytidae, Staphylinidae, Tenebrionidae.

<sup>3</sup> Includes Formicidae, Ichneumonidae, Tenthredinidae

<sup>4</sup> Includes Gelechiidae, Pryalidae

#### Arthropod Prey of Other Species

Eight families within seven orders of arthropods were identified in five fecal samples from MacGillivray's warblers (Table 4.5). Average size of adult arthropods

consumed by MacGillivray's warbler was 4.04 mm; average size of larvae consumed was 20.09 mm.

Three families were identified out of six orders of arthropods in four fecal samples from Pacific-slope flycatchers. I was able to estimate size only for beetles consumed by this species (Table 4.6). From the three fecal samples analyzed for Hammond's flycatchers, six orders and one family of arthropods were identified (Table 4.6).

Figure 4.2. Distribution of sizes of A) all arthropod prey and B) beetles consumed by Swainson's thrushes, Oregon Coast Range, 1996, 1997, 1999, 2000.

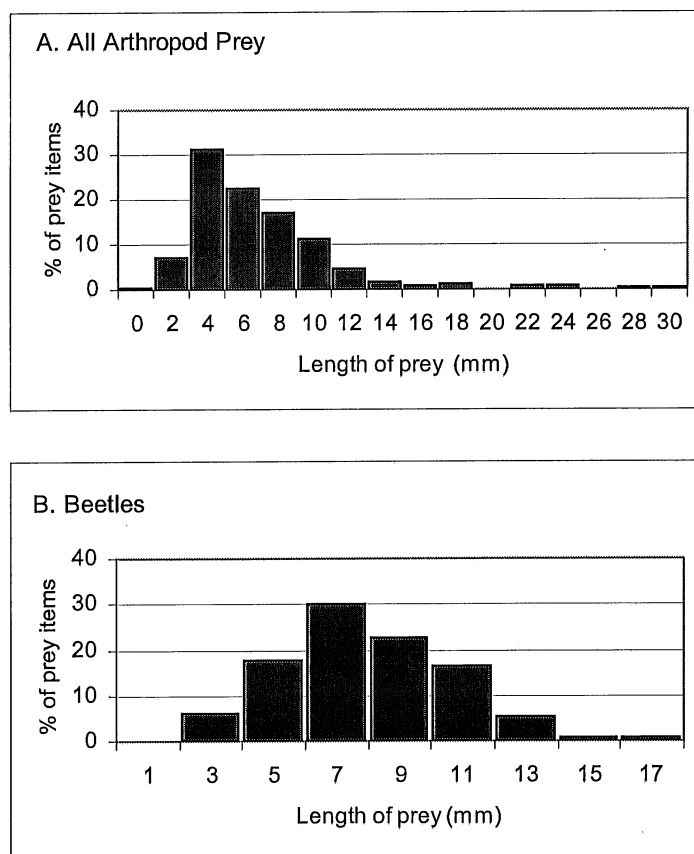




Figure 4.3. Percent of Swainson's thrush fecal samples with seeds from fruiting shrubs by 10-day period, Oregon Coast Range. Combined data from 1997, 1999, 2000 (n = 139 samples).

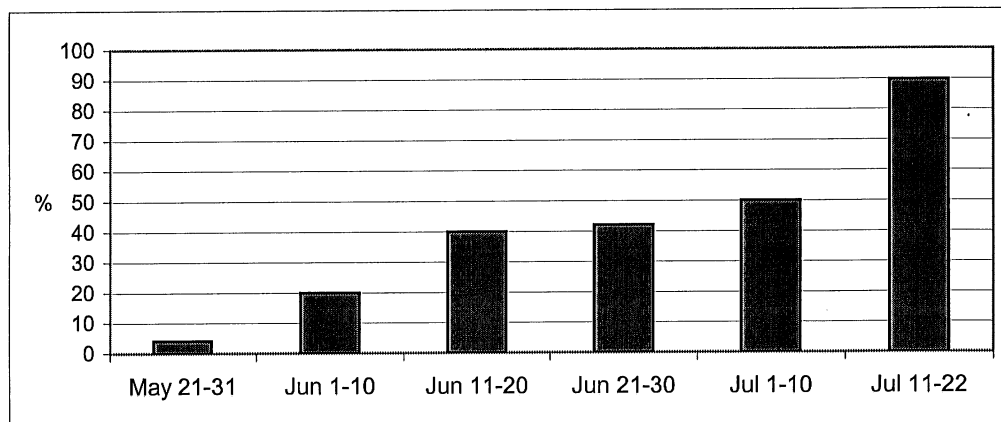


Table 4.5. Frequency of occurrence (number of fecal samples) and sizes (mm) of arthropod prey identified in MacGillivray's warbler fecal samples (n=5), Oregon Coast Range, 1999.

Order	Frequency for Order <sup>1</sup>	Family	Frequency for Family <sup>1</sup>	Size Mean (Range)	N <sup>2</sup>
Araneida	5	Linyphiidae	1	.	0
		Unknown spider	5	2.7 (2.6 - 2.8)	2
Coleoptera	5	Coccinellidae	1	.	0
		Curculionidae	1	.	0
		Scarabiidae	1	.	0
		Unknown beetle	5	6.44 (4.3 - 7.9)	4
		Unknown fly	4	3.13 (2.4 - 5.1)	8
Diptera	4	Chironomidae	1	.	0
		Unknown fly	4	3.13 (2.4 - 5.1)	8
Hemiptera	2	Tingidae	1	.	0
		Unknown Hemiptera	1	.	0
Homoptera	2	Unknown Homoptera	2	3.94 (2.5 - 5.4)	2
Hymenoptera	4	Diapriidae	1	.	0
		Formicidae	1	.	0
		Symphyta larva	1	19.03	1
		Unknown wasp	2	.	0
Lepidoptera	4	Unknown caterpillar	4	20.31 (11.0 - 27.1)	5
Unknown	4	Unknown	4	5.47 (4.0 - 7.0)	2

<sup>1</sup> Number of fecal samples in which taxa occurred out of five total.

<sup>2</sup> Number of fragments used to calculate length of prey item with regressions of body length as predicted by femur, tibia, or mandible length. Only whole leg segments were used to estimate body length.

Table 4.6. Frequency of occurrence and sizes (mm) of arthropod prey identified in fecal samples of Pacific-slope flycatchers (n=4) and Hammond's flycatchers (n=3), Oregon Coast Range, 1996, 1997, 1999.

Order	Pacific-slope Flycatcher			Hammond's Flycatcher		
	Freq. <sup>1</sup>	Size Mean (Range)	N <sup>2</sup>	Freq. <sup>1</sup>	Size Mean (Range)	N <sup>2</sup>
Araneida	3	.	0	1	.	0
Coleoptera	4	.	0	2	.	0
Chrysomelid	1	.	0	0	.	0
Scolytid	1	7.13 (3.4 -10.5)	5	0	.	0
Unknown beetle	4	.		2	8.18 (7.1 - 9.2)	2
Diptera	2	.	0	1	6.73	1
Hemiptera	1	.	0	1	.	0
Homoptera	1	.	0	2	.	0
Cicadellid	1	.		0	.	0
Cercopid	0	.		2	.	0
Hymenoptera (wasp)	1	.	0	2	4.17	1
Lepidoptera	0	.		2	11.53 (8.9 - 14.1)	2
Unknown arthropod	1	.	0	1	.	0

<sup>1</sup> Number of fecal samples in which taxa occurred.

<sup>2</sup> Number of fragments used to calculate length of prey item based on regressions predicting relationship of body length to femur, tibia, or mandible length. Only whole leg segments were used to estimate body length.

## Fruit in Bird Diets

### *Swainson's Thrushes*

Forty-one percent of the 139 fecal samples from Swainson's thrushes contained seeds from fruits. Seeds from seven species of plants were identified in the diet. Red huckleberry (*Vaccinium parvifolium*) was the most frequently consumed species, occurring in 18% of all fecal samples. Salal (*Gaultheria shallon*) was the second most frequently consumed, occurring in 12% of the fecal samples. Seeds from elderberry (*Sambucus* spp.) were found in 10% of the fecal samples, and blackberry seeds, including those of Himalayan (*Rubus discolor*) and trailing blackberry (*R. ursinus*), occurred in 9% of samples. The proportion of fecal samples containing seeds from fruits

increased throughout the season (Fig. 4.3). Blackberries were the only fruit represented in the Swainson's thrush diet throughout the entire sampling season, from 31 May to 22 July, although salal and red huckleberry were found in all but the first 10-day period.

### *Other Species*

Fecal samples from seven species in addition to Swainson's thrushes were examined for seeds: chestnut-backed chickadee (N=1), wrentit (N=2), hermit thrush (N=1), varied thrush (N=1), spotted towhee (N=2), song sparrow (N=4) and dark-eyed junco (N=15). Salal and *vaccinium* seeds were found in a spotted towhee fecal sample. Salal berries also were consumed by the wrentit. *Vaccinium* seeds were found in the varied thrush sample. Only one of the dark-eyed junco samples contained seeds, which were most likely of herbaceous origin.

### Arthropods on Understory Vegetation

Eighteen insect orders, nine non-insect arthropod taxa, and two mollusk taxa were identified from 28,448 individuals collected from 15 understory plant species from 1996–1999 (Appendix B). The most abundant taxa overall were aphids, collembolans, and two families of web-spinning spiders (Linyphiidae and Theridiidae; Table 4.7). Overall, the dominant taxa by weight included Geometrid caterpillars, and Linyphiid and Araneid spiders. However, the dominant taxa based on biomass varied with stand condition (Table 4.8).

### Plant Species Effects on Arthropods

Abundance intensity of all arthropod taxa pooled was  $\geq 5$  times higher on bracken fern than on the six other plant species sampled frequently enough to analyze (Fig. 4.4A). Biomass intensity of all arthropod taxa pooled also was high on bracken fern; only oceanspray supported a similar biomass (Fig. 4.4B). Western hemlock and vine maple supported the lowest arthropod prey intensity, in terms of both abundance and biomass.

Table 4.7. Average abundance intensity index (number of individuals/100 g dry plant material) with standard errors by stand age and condition for the three most abundant arthropod taxa sampled on 15 species of understory shrubs across eight sites in four years.

Abundance Rank	Overall	Mature	Group-Selection	Thinned	Unthinned
1	Homoptera: Aphididae 8.93 (2.01)	Collembola: Sminthuridae 7.61 (3.62)	Homoptera: Aphididae 46.76 (11.53)	Homoptera: Aphididae 14.33 (4.36)	Collembola: Entomobryidae 5.70 (0.87)
2	Collembola: Entomobryidae 4.88 (0.48)	Collembola: Isotomidae 5.30 (2.67)	Collembola: Isotomidae 16.30 (8.16)	Collembola: Entomobryidae 4.93 (0.65)	Araneida: Linyphiidae 4.65 (0.74)
3	Araneida: Linyphiidae 3.91 (0.35)	Araneida: Theridiidae 3.97 (0.80)	Araneida: Theridiidae 6.69 (4.07)	Psocoptera 4.00 (1.21)	Psocoptera 3.99 (1.33)

Table 4.8. Average biomass intensity index (mg arthropod / 100 g dry plant material) with standard errors by stand age and condition for the three most abundant arthropod taxa sampled on 15 species of understory shrubs across eight sites in four years.

Biomass Rank	Overall	Mature	Group-Selection	Thinned	Unthinned
1	Lepidoptera: Geometridae (larvae) 14.6 (3.35)	Lepidoptera: Geometridae 29.0 (13.26)	Homoptera: Aphididae 90.8 (52.80)	Homoptera: Aphididae 14.9 (4.17)	Araneida: Linyphiidae 16.1 (2.11)
2	Araneida: Linyphiidae 11.9 (1.07)	Spirobolida 20.3 (13.72)	Lepidoptera: Geometridae 64.7 (20.58)	Araneida: Theridiidae 12.2 (1.99)	Araneida: Araneidae 15.1 (2.25)
3	Araneida: Araneidae 10.9 (1.13)	Araneida: Araneidae 11.4 (2.21)	Raphidioptera: Raphidiidae 42.5 (18.44)	Homoptera: Cercopidae 11.6 (3.50)	Lepidoptera: Geometridae 11.9 (3.28)

Intensity of large Lepidoptera larvae (>6 mm) differed among plant species (abundance:  $P = 0.01$ , biomass:  $P = 0.04$ , Kruskal-Wallis test). Oceanspray and hazel had the highest mean scores for both intensity variables; the sum of scores for vine maple and western hemlock also were higher than expected under a null hypothesis of no difference among plant species (Table 4.9). The two fern species and salal scored

lower than expected for both intensity variables, with sword fern scoring the lowest of all seven plant species.

Abundance intensity of Homoptera ( $>2$  mm) was 17 times higher on bracken fern than on the shrub species with the next highest abundance, hazel (Fig. 4.5A). Biomass intensity of Homoptera was almost 10 times higher on bracken fern than on the shrub with the next highest biomass, salal (Fig. 4.5B).

Intensity of large Diptera ( $>3$  mm) varied among plant species ( $P \leq 0.01$ , Kruskal-Wallis test). Bracken fern and oceanspray supported the greatest abundance and biomass intensity of large Diptera, whereas hemlock and hazel had the lowest scores (Table 4.10).

Abundance intensity of adult beetles ( $>3$  mm) differed significantly among plant species ( $P = 0.003$ , Kruskal-Wallis test.) Oceanspray, vine maple, bracken fern, and sword fern all scored higher than expected under a null hypothesis of no difference among plant species, whereas hazel scored close to expected (Table 4.11). In contrast, hazel had the highest score for biomass intensity. Vine maple, oceanspray, bracken fern, and sword fern also scored higher than expected for biomass intensity of beetles. Salal and western hemlock scored lower than expected for both intensity variables of beetles.

Figure 4.4. A) Median abundance intensity index (number of individuals/ 100 g dry plant material) and B) biomass intensity index (mg / 100 g dry plant material) with 90% confidence limits of arthropod prey for Wilson's warblers (Coleoptera and Diptera >3 mm, larva >6 mm, and all other taxa >2 mm) for seven understory plant species in the Oregon Coast Range. Two plant species differ significantly in intensity if 90% confidence limits of one do not overlap the median of the other. Plant species and sample size are: ACCI = vine maple (51), COCO = California hazel (10), GASH= salal (49), HODI = oceanspray (11), POMU = sword fern (34), PTAQ = bracken fern (24), and TSHE = western hemlock (32).

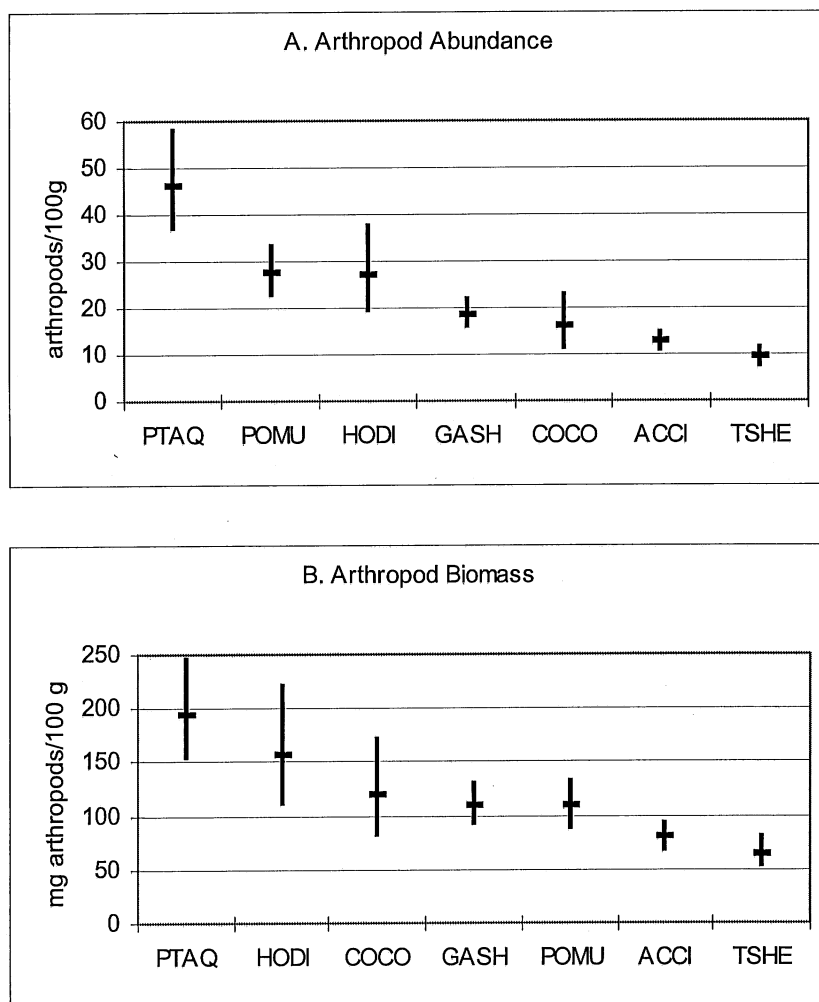


Figure 4.5. A) Median abundance intensity (number of individuals / 100g plant weight) and B) biomass intensity indices (mg arthropod/100 g plant weight) with 90% confidence limits for **Homoptera** on seven species of understory vegetation in thinned, unthinned, and mature Douglas-fir stands in the Oregon Coast Range. Plant species and sample size are: ACCI = vine maple (51), COCO = California hazel (10), GASH= salal (49), HODI = oceanspray (11), POMU = sword fern (34), PTAQ = bracken fern (24), and TSHE = western hemlock (32).

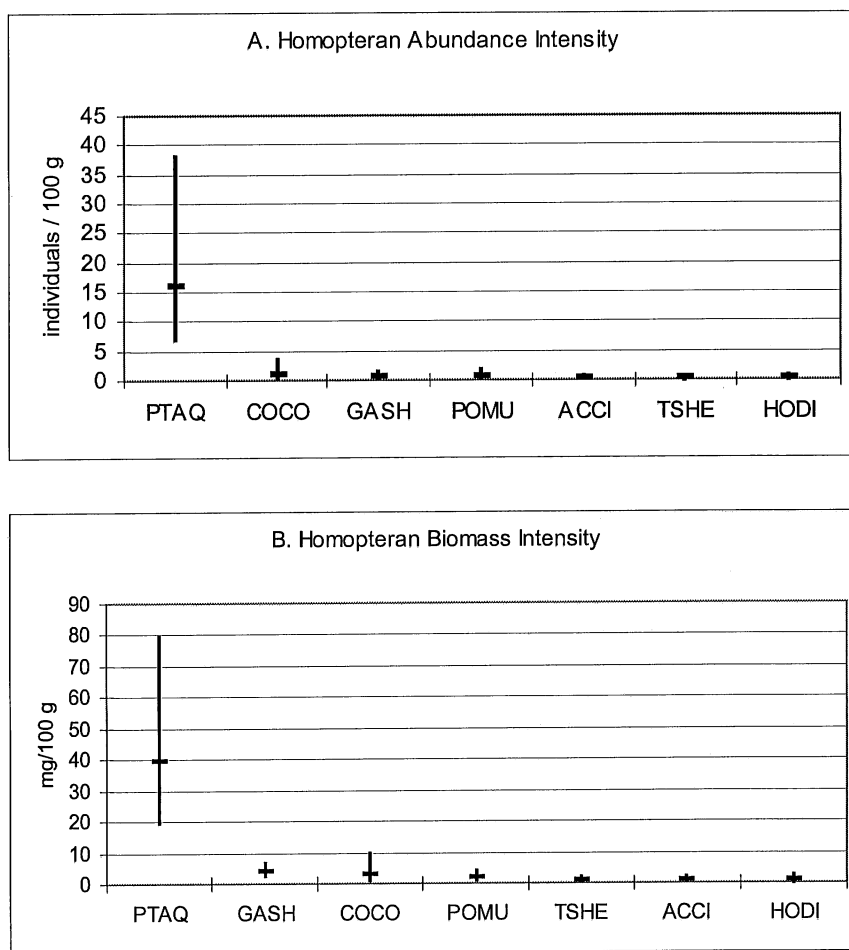


Table 4.9. Wilcoxon Scores (Rank Sums) for abundance and biomass intensity of **lepidoptera larvae** >6 mm in length on seven understory plant species. Mean scores in bold were higher than expected under the null hypothesis of no difference in intensity among plant species (Kruskal-Wallis test).

Plant Species	N <sup>1</sup>	Abundance Index			Biomass Index		
		Sum of Scores	Expected Under H <sub>0</sub>	Mean Score	Sum of Scores	Expected Under H <sub>0</sub>	Mean Score
Oceanspray	11	1606	1160	<b>146</b>	1523	1160	<b>138</b>
California hazel	10	1330	1055	<b>133</b>	1309	1055	<b>131</b>
Vinemaple	50	5506	5275	<b>110</b>	5461	5275	<b>109</b>
Western hemlock	32	3475	3376	<b>109</b>	3541	3376	<b>111</b>
Bracken fern	24	2484	2532	103	2462	2532	103
Salal	49	4900	5169	100	4997	5169	102
Sword fern	34	2854	3587	84	2862	3587	84

<sup>1</sup> N is the number of samples for each plant species pooled across four years and eight sites (not all sites were sampled each year).

Table 4.10. Wilcoxon Scores (Rank Sums) for abundance and biomass intensity of **flies** >3 mm on seven understory plant species, in descending order of mean score. Mean scores in bold were higher than expected under the null hypothesis of no difference in intensity among plant species (Kruskal-Wallis test).

Plant Species	N <sup>1</sup>	Abundance Index			Biomass Index		
		Sum of Scores	Expected Under H <sub>0</sub>	Mean Score	Sum of Scores	Expected Under H <sub>0</sub>	Mean Score
Bracken fern	24	3202	2532	<b>133</b>	3171	2532	<b>132</b>
Oceanspray	11	1329	1160	<b>121</b>	1264	1160	<b>115</b>
Vinemaple	50	5503	5275	<b>110</b>	5579	5275	<b>112</b>
Salal	49	5386	5169	<b>110</b>	5207	5169	<b>106</b>
Sword fern	34	3513	3587	103	3645	3587	<b>107</b>
Western hemlock	32	2499	3376	78	2595	3376	81
California hazel	10	721	1055	72	692	1055	69

<sup>1</sup> N is the number of samples for each plant species pooled across four years and eight sites (not all sites were sampled each year).

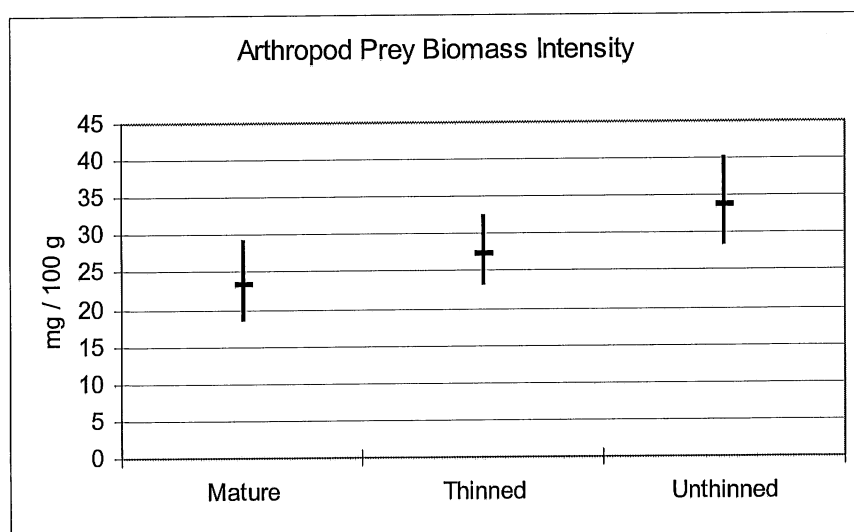


Table 4.11. Wilcoxon Scores (Rank Sums) for abundance and biomass intensity of **beetles** >3 mm on seven understory plant species, in descending order of mean score. Mean scores in bold were higher than expected under the null hypothesis of no difference in intensity among plant species (Kruskal-Wallis test).

Plant Species	N <sup>1</sup>	Abundance Index			Biomass Index		
		Sum of Scores	Expected Under H <sub>0</sub>	Mean Score	Sum of Scores	Expected Under H <sub>0</sub>	Mean Score
Oceanspray	11	1369	1160	<b>124</b>	1245	1160	<b>113</b>
Vinemaple	50	6031	5275	<b>121</b>	6195	5275	<b>124</b>
Bracken fern	24	2878	2532	<b>120</b>	2645	2532	<b>110</b>
Sword fern	34	4017	3587	<b>118</b>	3779	3587	<b>111</b>
California hazel	10	1054	1055	105	1319	1055	<b>132</b>
Salal	49	4587	5169	94	4435	5169	90
Western hemlock	32	2217	3376	69	2535	3376	79

<sup>1</sup> N is the number of samples for each plant species pooled across four years and eight sites (not all sites were sampled each year).

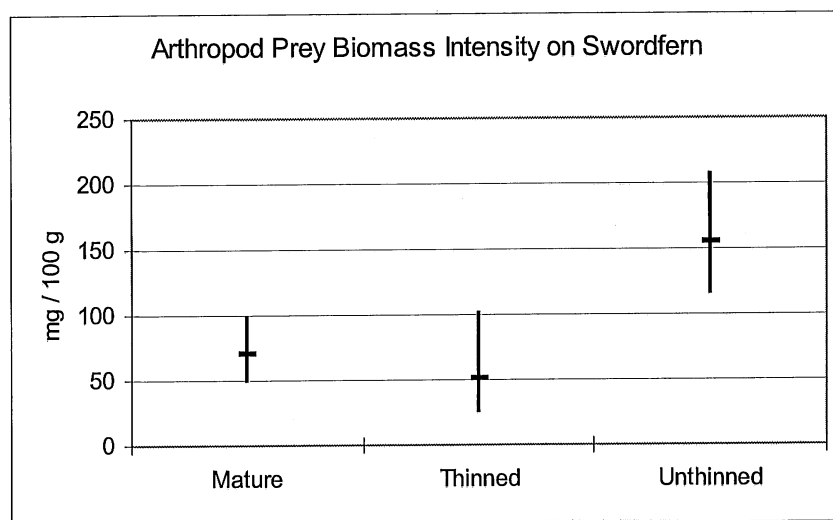
Figure 4.6. Median biomass intensity index with 90% confidence limits (mg arthropod /100g dry plant weight) for arthropod prey for Wilson's warblers (Coleoptera and Diptera >3 mm, larvae >6 mm, and all other taxa >2 mm) on understory vegetation in three Douglas-fir stand types in the Oregon Coast Range.



### Stand Condition Effects on Arthropods

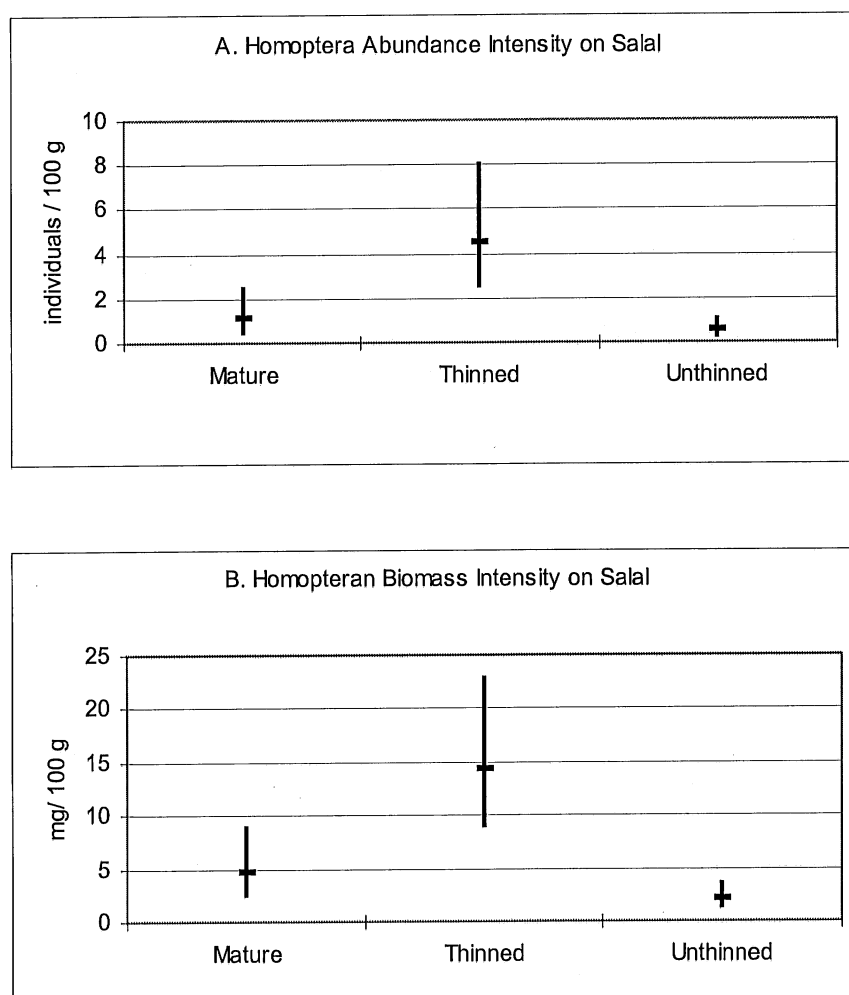
Abundance intensity of arthropods did not differ among mature, young thinned, and young unthinned stand conditions for all plant species pooled ( $P = 0.27$ , ANOVA), nor for any of the four plant species adequately sampled in each stand condition (vine maple, salal, oceanspray, sword fern;  $P > 0.10$ , ANOVA). Biomass intensity of all arthropod prey for Wilson's warblers pooled differed among stand conditions for all plant species pooled ( $P = 0.08$ , ANOVA; Fig. 4.6). Arthropod biomass intensity on sword fern was 2.2 times greater ( $P = 0.005$ , ANOVA) in unthinned than mature stands and 3 times higher in unthinned than in thinned (Fig. 4.7).

Figure 4.7. Arthropod biomass intensity index with 90% confidence limits (mg arthropod/100 g dry plant weight) for arthropod prey for Wilson's warblers (Coleoptera and Diptera >3 mm, larva >6 mm, and all other taxa >2 mm) on **sword fern** in three Douglas-fir stand types in the Oregon Coast Range.



Neither abundance nor biomass intensity of Lepidoptera larvae differed among stand conditions for all plant species pooled ( $P > 0.28$ , Kruskal-Wallis test), nor for vine maple, salal, oceanspray, or sword fern ( $P \geq 0.65$ , Kruskal-Wallis test). Homoptera intensity in terms of both abundance and biomass was greater on salal in thinned stands than on salal in mature or unthinned stands ( $P < 0.04$ , Kruskal-Wallis test; Fig. 4.8).

Figure 4.8. A) Median abundance intensity (number of individuals / 100g plant weight) and B) biomass intensity indices (mg arthropod/100 g plant weight) for **Homoptera** on salal in thinned, unthinned, and mature Douglas-fir stands in the Oregon Coast Range.



Ranked abundance intensity of large Diptera did not differ among mature, thinned, and unthinned stand conditions for all plant species pooled. Abundance intensity of Diptera was greater in unthinned than in thinned and mature stands for sword fern ( $P = 0.02$ , Kruskal-Wallis test) and salal ( $P = 0.03$ , Kruskal-Wallis test). Biomass intensity of Diptera did not differ among stand conditions ( $P = 0.31$ , Kruskal-Wallis test). Beetle abundance intensity was greatest in unthinned stands for all plant species pooled ( $P = 0.08$ , ANOVA; Fig. 4.9A). Abundance intensity of beetles on salal was 6.25 times higher in unthinned stands than in thinned. Similarly, median beetle abundance intensity on sword fern was more than 10 times greater in unthinned than in thinned and mature. Biomass intensity of beetles showed a similar pattern to abundance, and was greatest in unthinned stands (Fig. 4.9B). When tested separately by plant species, biomass intensity of beetles was 5.3 times greater on salal in unthinned than thinned stands. On sword fern, beetle biomass intensity was 24 times higher in unthinned than in thinned stands, and 8.7 times higher in unthinned than mature stands.

Although intensity of some arthropod prey groups was greatest on individual plants in unthinned stands, accounting for shrub cover at the stand level resulted in greater estimates of overall abundance in thinned than in unthinned and mature stands (Fig. 4.10A). Cover-weighted biomass also was greatest in thinned stands, although the slight overlap of the upper confidence interval for unthinned stands with the mean of that in thinned provided only weak evidence for a statistical difference (Fig. 4.10B). No consistent relationship between stand condition, shrub cover, and stand-level arthropod abundance or biomass was evident across individual study sites (Table 4.12).

Figure 4.9. A) Median abundance (number of individuals / 100g plant weight) and B) biomass indices (mg arthropod / 100 g plant weight) for Coleoptera on salal, swordfern, and across pooled plant species in thinned, unthinned, and mature Douglas-fir stands in the Oregon Coast Range.

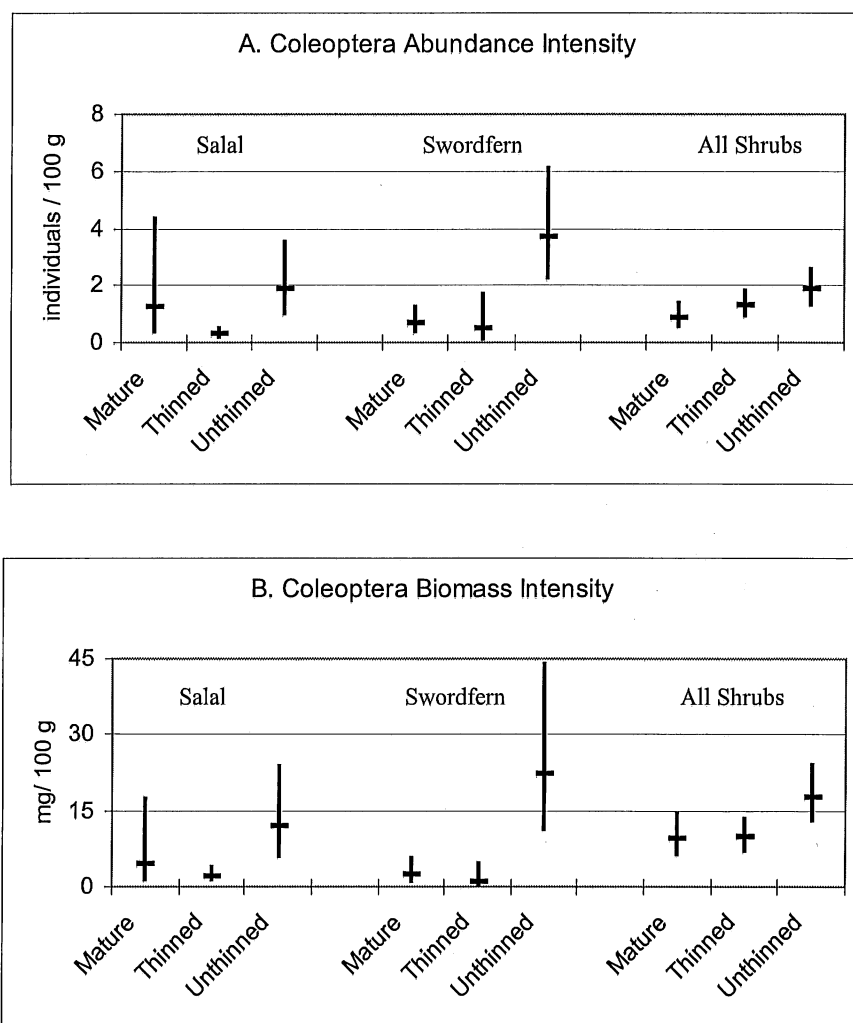


Figure 4.10. Median cover-weighted abundance (A) and biomass (B) indices with 90% confidence intervals for arthropod prey on understory shrubs in three stand conditions in the Oregon Coast Range.

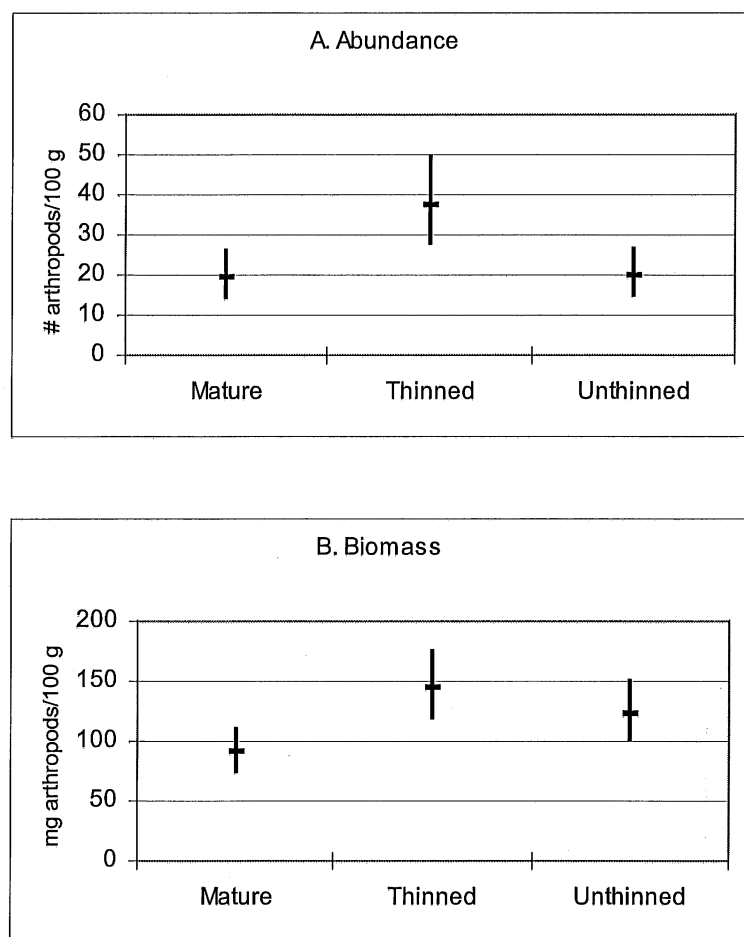


Table 4.12. Average abundance (number of individuals/ 100 g dry plant material) and biomass (mg arthropod/ 100 g dry plant material) indices weighted by shrub cover, and average cover of low shrubs and tall, deciduous shrubs in 13 Douglas-fir stands in the Oregon Coast Range.

Site	Condition	Abundance	Biomass	Low Shrub (%)	Tall Shrub (%)
D-Line	Mature	29.04	85.66	56	10
	Thinned	52.70	178.77	99	20
	Unthinned	21.40	113.52	57	8
Mary's Peak	Mature	69.11	329.86	45	13
	Thinned	69.62	218.38	41	16
	Unthinned	16.17	87.84	70	65
Sand Creek	Mature	25.98	113.91	98	40
	Thinned	18.40	138.60	18	28
	Unthinned	59.76	327.01	72	34
Lewisburg Saddle	Group Selection	59.67	377.48	57	40
	Mature	15.13	122.33	49	15
Peavy	Group Selection	68.52	180.81	52	6
	Mature	18.35	116.33	46	5

## DISCUSSION

### Bird Diets

Many insectivorous passerines prefer certain taxa, but will prey on a wide range of arthropod orders (Beaver and Baldwin 1975, Sample et al. 1993). This appeared to be true for Wilson's warblers, which are known to eat a relatively large variety of insect taxa (Beal 1907, Raley and Anderson 1990), but most frequently consumed caterpillars, homopterans, flies, and beetles. The number of arthropod orders ( $>6$ ) found in relatively small samples for MacGillivray's warblers, Pacific-slope and Hammond's flycatchers is consistent with the literature indicating their lack of prey specificity (Beaver and Baldwin 1975, Pitocchelli 1995). Regardless of taxa, arthropods  $\leq 2$  mm in length were infrequently found in the diets of the birds I examined, even though this size class was very abundant on understory vegetation. Arthropods  $< 2$  mm in length are seldom taken even by winter wrens (Van Horne and Bader 1990), one of the smallest of the avian insectivores that feeds in the forest understory. Wilson's warblers select prey  $> 3$  mm (Raley and Anderson 1990). Arthropods  $> 24$  mm in length also occurred rarely in diets of the birds I studied. However, arthropods that exceeded the maximum lengths found in bird diets were rare on the vegetation I sampled.

### *Wilson's Warblers*

The complexity of forest vegetation hampers the ability to accurately quantify food resources that are actually available to birds (Morrison et al. 1990). I attempted to minimize this problem by focusing on understory vegetation and the birds primarily associated with this vertical layer in forests. Wilson's warblers are known to forage to the maximum height of the available vegetation (Stewart et al. 1977), and 25% of the foraging activity I observed occurred above the layer of vegetation that I sampled for arthropods (Chapter 3). Thus, I did not measure all prey available to Wilson's warblers. High abundance in mid-story or canopy vegetation of any taxa that appeared to be used more than expected based on availability in the understory (forage ratio  $> 1$  in Table 4.2) would belie their selection as prey.



In addition, my sampling method may have underestimated some arthropod prey. Beating foliage to dislodge arthropods was an adequate method for sampling free-living, sedentary prey items available to birds, but organisms such as miners and borers would have been inadequately sampled because I did not visually inspect for organisms that may have been attached to vegetation. However, these organisms offer less food value to many species of insectivorous birds because of their relative inaccessibility (Holmes and Schultz 1988). Arthropod eggs also may not have been well sampled with the method of beating shrubs. However, the low frequency of occurrence of arthropod eggs in both diet ( $\leq 15\%$ ) and shrub samples may indicate that Wilson's warblers foraged opportunistically on arthropod eggs when encountered, but did not necessarily select for them. I recommend a combination of shrub beating and aerial insect traps to sample food resources for Wilson's warblers and other species that use perch- and hover- gleaning foraging strategies.

In spite of these limitations, I believe that Wilson's warblers were selectively consuming Lepidoptera larvae, Diptera, and Coleoptera. Most species of Lepidoptera are generally uncommon in coniferous forests in the Pacific Northwest (Parsons et al. 1991), including the canopy of old-growth Douglas-fir (Voegtlin 1982, Schowalter and Ganio 1988), so it is unlikely that their abundance increased above the layer of vegetation I sampled. Furthermore, Lepidoptera larvae are known to be especially important prey for many neotropical migrant species that breed in temperate forests (Holmes et al. 1979, Graber and Graber 1983, Sample et al. 1993). Lepidopteran and sawfly larvae also were consumed by MacGillivray's warblers, Swainson's thrushes, and Hammond's flycatchers. As the largest food items consumed by Wilson's warblers and other birds, and the dominant arthropod prey group by weight across all sites and stand conditions, Lepidoptera larvae probably represented a critical source of energy for birds on my study sites. In addition, caterpillars and sawfly larvae have high calcium concentrations relative to many other arthropod groups (Schowalter and Crossley 1983), providing insectivorous birds with an essential resource for egg-laying.

The importance of Diptera in the diet that I observed is supported by the foraging strategy of Wilson's warblers and by published accounts. A large proportion of

flies in the diet reflects the hover-gleaning and aerial fly-catching foraging strategy frequently used by Wilson's warblers (Bent 1963, Stewart et al. 1977). Active, flying insects such as adult flies and wasps likely were under-sampled with the foliage beating method I used to estimate available arthropod prey. If flies were indeed under-sampled, in both understory and overstory vegetation, they may have been more available than estimated, and therefore may not have been selected as prey by Wilson's warblers. However, the selection of Diptera by Wilson's warblers that I observed is consistent with the findings of Raley and Anderson (1990) for Wilson's warblers foraging in montane willow habitats.

A high frequency of Coleoptera in the diet relative to that on shrubs is consistent with a preferential selection of Coleoptera as prey by Wilson's warblers reported by Raley and Anderson (1990). Raley and Anderson (1990) collected stomachs from birds and were able to identify Cantharidae as a large proportion of the Coleoptera eaten. Using fecal analysis, I was not often able to identify arthropods to the family level. Nonetheless, I also identified Cantharidae, as well as Mordellidae, in Wilson's warbler diets. Adult Cantharids are common on foliage, soft-bodied, and mostly 5 – 15 mm in length (Borror et al. 1989). These characteristics make them an optimal prey item for Wilson's warblers. Mordellids also are common on foliage, but unlike Cantharids, they tend to move rapidly or take flight when alarmed (Borror and White 1970), possibly making them a less efficient prey item. I identified fragments of Mordellids in only 2 out of 96 Wilson's warbler fecal samples.

Although Homoptera occurred more frequently in Wilson's warbler diets than on understory shrubs, there is little evidence to support the selection of this insect group as prey. Homoptera are common to abundant throughout forest canopies (Parsons et al. 1991, Schowalter and Ganio 1998), and could have been consumed opportunistically as they were encountered. Raley and Anderson (1990) found that Homoptera ranked lowest in preference of all prey groups consumed by Wilson's warblers in a montane willow habitat. However, Homoptera and other arthropod groups that were not used disproportionately to their availability by Wilson's warblers in my study, such as spiders and adult hymenoptera, should not be considered unimportant as prey. These taxa

occurred in  $\geq 40\%$  of the Wilson's warbler fecal samples I examined, and may function as staples in the diet. Furthermore, birds may rely more heavily on non-preferred prey items when preferred taxa are scarce (Sample et al. 1993).

### *Swainson's Thrushes*

The generalized diet that I recorded for Swainson's thrushes, including fruit as well as many arthropod taxa, has been documented for this species from various parts of the breeding range (Mack and Yong 2000). The variety of arthropod taxa in the diet reflects the varied foraging strategies used by Swainson's thrushes. The inclusion in the diet of ground-dwelling taxa, such as carabid beetles, indicates the tendency of this species to spend a significant amount of foraging time on the ground. The methods I used to sample arthropod prey did not include ground-dwelling arthropods. However, some prey, such as Homopterans and sawfly larvae, were most likely gleaned from foliage while foraging throughout the vertical profile of the forest (Holmes and Robinson 1988).

Although I was unable to adequately sample prey availability for Swainson's thrushes, the importance of beetles and ants is evident from my observations and is supported by the findings of others (Mack and Yong 2000). Several beetle taxa that were preyed on by Swainson's thrushes, including Buprestidae and Elateridae, and some species of ants are associated with dead and dying wood (Borror et al. 1989). The presence of crane flies, another taxa often associated with decaying wood, in Swainson's thrush diets also was recorded by Beal (1915) from stomach samples. Woody debris may therefore be an important habitat element for Swainson's and other thrushes with similar foraging habits and diets (e.g., hermit and varied thrushes).

Fruit becomes an increasingly important food for Swainson's thrushes, as well as many other species of omnivorous passerines, late in the breeding season as birds prepare for migration from breeding to wintering grounds (Parrish 1997, Mack and Yong 2000). Increased availability (Fire Effects Information System [online], personal observation) and consumption (Fig. 4.3) of fruit was apparent by mid-July in my study area, with red huckleberry, salal, elderberry, and blackberry as the primary sources of

mast for thrushes. An increase in fruit availability coincides with decreasing abundance of insects, so fruit may function as an alternative food resource to preferred insect prey. For some long-distance migrants however, fruit may actually be required in order to acquire sufficient energy reserves for successful migration (Martin 1985, Blake and Loiselle 1992). A dietary shift from primarily insects to fruit may confer an energetic advantage because frugivory facilitates energy storage in the form of fat reserves (Parrish 1997). The importance of fruit and fruit-bearing shrubs to the survival of Swainson's thrushes and other frugivorous migrants should therefore not be underestimated.

## Distribution of Food Resources

### *Effect of Plant Species*

Common understory plant species varied in abundance and biomass of arthropod prey for songbirds. Herbivorous insect species often are associated with a narrow range of plant taxa, thus defining characteristic assemblages of arthropods on each plant species (Schowalter 2000). Even though I was not able to identify most arthropods below the taxonomic level of family, I found differences among plants species even for the much coarser prey categories I analyzed. Many of the differences I found can be explained by a dichotomy between deciduous and evergreen plant species. In general, deciduous species supported a higher intensity of the arthropods that were important prey for birds than did evergreen species.

Tall deciduous shrubs were important sources of arthropod prey, particularly Lepidoptera larvae. While conifers may support high abundances of lepidopteran larvae, especially during outbreaks (Furniss and Carolin 1977) a large proportion of the lepidopteran diversity in western forests is associated with deciduous trees and shrubs (Hammond and Miller 1998). Because populations of forest insect species can fluctuate dramatically among generations, prey diversity provides a stable resource for generalist insectivores over time (Jackson 1979). I was unable to assess lepidopteran diversity on the plants I sampled, but I found that tall, deciduous shrubs such as oceanspray, California hazel, and vine maple supported the highest intensity of lepidopteran larvae

of the understory plant species I sampled. Although western hemlock in the forest understory also was a potential source of lepidopteran larvae for birds, it supported low levels of all other prey categories. Oceanspray may be particularly important in supporting prey for birds because it supports both a high diversity and a high abundance of Lepidoptera (Muir et al. 2002). Oceanspray also supported relatively high intensity of all prey taxa pooled, a high abundance of beetles, and the highest abundance of flies.

Vine maple has not been noted for a high diversity of Lepidoptera larvae (Oboyski 1996, Muir et al. 2002). However, Braun et al. (2002) calculated that folivory by 22 lepidopteran taxa on vine maple in western Washington was equal to 66% of the folivory on the three overstory conifers. This high rate of folivory on a shrub that is common throughout the Pacific Northwest suggests that vine maple may support a significant prey resource for insectivorous birds in the region. On my study sites, vine maple supported a relatively high intensity of prey taxa important in the diet of Wilson's warblers: Lepidoptera larvae, beetles and flies. The high frequency of foraging on vine maple by Wilson's and MacGillivray's warblers (Chapter 3) provides further evidence of the value of this shrub as a source of prey.

Bracken, a fern that grows new fronds each spring from perennial rhizomes, supported a notably high intensity of flies, beetles, and all prey taxa pooled relative to other understory plants. Bracken fern supports a high abundance of herbivores and their associated predators (Lawton 1976), especially where it grows in large, dense patches in sunlit areas (Doolittle 2000). Bracken fern was distinguished from other understory species by exceptionally high abundance intensity of several arthropod groups found in diets of Wilson's warblers and other bird species: aphids, ants, coccinellid beetles, Tenthredinidae (sawfly) larvae, and Cercopidae (Homoptera) (Doolittle 2000). A relatively high abundance but low biomass of arthropods on swordfern reflected an arthropod assemblage dominated by small detritivores such as Psocoptera and Collembola (Doolittle 2000) that were not important in bird diets.

*Effect of Stand Condition/ Management History*

Because forest management influences the structure and composition of vegetation communities, it was difficult and unrealistic to completely separate the effects on arthropods of plant species composition from those of management history. Abundance and cover of many of the understory species I studied are known to respond to management-induced changes in the density and cover of overstory trees. By increasing resource availability, partial removal of the overstory favors several of the shrubs that supported the most arthropod prey (Bailey et al. 1998, Thomas et al. 1999), whereas the light-depauperate understory of unthinned stands tends to be dominated by species that were less important in providing food resources for birds. For example, bracken fern, a species that supported high arthropod prey loads, can become abundant following disturbances such as thinning (Crane 1990). As a shade-intolerant pioneer and seral species, bracken fern has been proposed as an indicator of light intensity (Emmingham 1972). In western Oregon, cover of bracken fern is more extensive in thinned stands than in unthinned and mature stands, where cover is typically low or negligible (Bailey et al. 1998, Doolittle 2000, Muir et al. 2002). In contrast, sword fern tends to be most abundant in young unthinned stands compared to thinned and mature conditions (Bailey et al. 1998). While probably not an important source of arthropods that are prey for birds, sword fern is used for nesting by some species that are associated with the understory, including Wilson's warblers (Chambers, pers. comm.), rufous hummingbirds, and varied thrushes (pers. obs.).

The tall, deciduous shrubs that were an important source of arthropod prey (oceanspray, hazel, and vine maple) are moderately shade tolerant and frequently occur under closed canopy. However, they can achieve greater cover and density under incomplete canopy and generally respond positively to reduction of overstory cover (O'Dea et al. 1995, Thomas et al. 1999, Thysell and Carey 2000). O'Dea et al. (1995) found higher rates of vine maple clone expansion and vegetative reproduction in thinned than unthinned Douglas-fir stands, and concluded that thinning can potentially increase vine maple density. Bailey et al. (1998) described vegetation at 28 sites in western Oregon, including two of the triads I sampled (see Methods), and found that tall

shrub cover, density, and leaf area index was greater in thinned than in unthinned stands. Oceanspray and hazel supported more prey than vine maple and were more influential in habitat selection by Wilson's and other shrub-associated warblers (Chapter 3). On my study sites, oceanspray cover was significantly greater in thinned and hazel cover was greater in GS compared to unthinned stands (Chapter 2). Thinned stands are therefore more likely than unthinned stands to provide suitable foraging habitat for Wilson's and MacGillivray's warblers, and dense thickets used by Swainson's thrushes for foraging and nesting (Dowlan 2003a, Hagar 2003a, 2003b).

The significantly greater intensity of arthropods on some species of understory plants in unthinned stands indicated that concentrations of some arthropod groups were greater on individual plants in unthinned stands relative to thinned and mature forest (Figs. 4.6, 4.7, 4.9), but did not mean that prey abundance was greater in unthinned stands. My indices of abundance and biomass intensity were standardized by unit weight of foliage, so significantly greater density, cover, and leaf area index of shrub foliage in thinned stands (Bailey et al. 1998, Chapter 2) translated to greater overall prey abundance and biomass (Fig. 4.10). One or a combination of the following hypotheses may best explain high arthropod intensity on shrubs in unthinned stands. First, some of the understory shrubs I sampled in unthinned stands may have been stressed as a result of competition for light and other resources. Greater physiological stress of plants may have made them more susceptible to herbivores (Schowalter 1985). Plants experiencing physical stress may be prone to high abundances and outbreaks of leaf-feeding insects (Stoszek et al. 1981, Berryman 1986). Arthropod predators can respond to high herbivore abundance with increased density (Halaj et al. 1998, Schowalter 2000:199), creating high overall arthropod abundance. Secondly, some herbivores are positively affected by density and patch size of host plants and negatively affected by diversity of surrounding plants (Strong and Lawton 1984). Thus, the relatively low richness of understory plant species in unthinned stands compared to thinned stands (Bailey et al. 1998) may have fostered high herbivore intensity. Sword fern and salal were dominant shrubs in unthinned stands and tended to occur in large, continuous patches. In the other stand types, small patches of these species were

scattered throughout a more diverse plant community. This distribution may have influenced the higher arthropod intensity in unthinned stands. Doolittle (2000) found negative relationships between surrounding shrub diversity and abundance of arthropods on salal. Thirdly, predation rates on insects may have been different among stand types. Predation by birds has significant effects on population dynamics of forest insects (Holmes et al. 1979, Otvos 1979). Wilson's, MacGillivray's, and orange-crowned warblers were the main foliage-gleaning species on understory vegetation, but they were virtually absent from unthinned stands (Chapter 2, Chapter 3). A lack of predation pressure from these species may have permitted greater intensity of prey species such as aphids (Doolittle 2000). Habitat in unthinned stands was probably unsuitable for understory foliage-gleaners because of sparse cover of tall deciduous shrubs that are used for foraging (Chapter 3) and nesting (Dillingham 2003, Dowlan 2003a, Hagar 2003a, 2003b). Finally, shrubs growing in the understory of unthinned stands may have had higher nutritional quality for herbivorous arthropods than those in the higher light environment of partially harvested stands. Under conditions of limited carbon availability (e.g., heavy shade), tannin production may be decreased (Coley et al. 1985) whereas nitrogen and water concentrations in plant tissues may increase (Barry and Foss 1983, Fales 1984). Increased tannin production by understory plants in clear-cuts compared to old-growth stands was associated with lower availability of crude protein for ungulate herbivores (Happe et al. 1990).

Cover and productivity of fruit- and seed-bearing understory plants also are influenced by characteristics of forest overstory structure (Alaback and Herman 1988, O'Dea et al. 1995, Klinka et al. 1996, Huffman and Tappeiner 1997). For example, by increasing resources available to understory plants, commercial thinning may result in an increase in their cover and biomass (Bailey et al. 1998, Thomas et al. 1999). Kerns et al. (in press) examined huckleberry abundance on some of the same sites I studied in the Oregon Coast Range, and found that thinned stands had significantly greater density of red huckleberry than unthinned. Furthermore, fruit production by huckleberry can increase where overstory cover is reduced (Minore 1984) or removed (Vance et al. 2001). Similarly, Bunnell (1990) found that salal seldom flowered under forest canopy



cover >33%, leading him to suggest that salal growing under a canopy is unlikely to provide food for frugivorous wildlife. Red elderberry also decreases in cover with increasing conifer overstory cover, rarely fruits under a forest canopy, and is favored by thinning (Crane 1989). Increased availability of mast from understory vegetation in thinned stands may explain the positive response of several bird species that include fruit in their diet (e.g., Swainson's thrush, Townsend's solitaire, western tanagers, and spotted towhees) to thinning (Muir et al. 2002, Hayes et al. 2003, Hagar and Howlin, submitted).

### Conclusions and Management Implications

Traditionally, understory vegetation, particularly woody shrubs, has not been favored in management practices aimed at timber production. Instead, the goal of standard vegetation management, using herbicides or manual methods, is to reduce cover of understory vegetation in order to minimize competition with crop trees (Burhill et al. 1989). Indeed, forest practice regulations require landowners to control non-conifer vegetation as a means of ensuring successful conifer regeneration after clear-cut harvests (Oregon Department of Forestry 2001). Even commercial thinning has been conventionally implemented at sufficiently low intensities to discourage response by the understory. As a result of these and other management practices, shrub and hardwood tree cover in the Oregon Coast Range has declined over the past five decades, and is likely to decrease further on federal forest lands as a result of reduced harvesting (Kennedy and Spies, submitted). However, a change in forest management goals on public lands and an evolving awareness of the importance of diversity in achieving sustainable resource outputs is driving a new appreciation for the value of understory vegetation.

Understory vegetation is a significant component of floristic and structural diversity in conifer-dominated forests (Halpern and Spies 1995). Although conifer regeneration and shrubs each contribute to vertical structure, there are important functional difference, particularly between conifers and deciduous shrubs and trees. Some obvious differences include different growth forms, leaf chemistry, phenology,

and reproductive strategies. The presence of shrubs and deciduous trees increases habitat heterogeneity in conifer-dominated forests, contributing to the diversity of niches available for birds and resulting in greater bird species diversity (Willson 1974, Willson and Comet 1996a, Hobson and Bayne 2000). Therefore, a forest stand that has multiple layers of coniferous foliage does not support as diverse a bird assemblage as one that has both deciduous and coniferous layers.

My findings illustrate the importance of understory vegetation, particularly tall, deciduous shrubs, in supporting arthropod prey and mast for songbirds. Vine maple, hazel, and oceanspray also provide resources for other wildlife species. Vine maple is a preferred food of deer and elk, and small mammals as well as birds consume its seeds, buds and flowers (Uchytel 1989). California hazel provides browse for big game, its nuts are a staple of food of several small mammal species and Steller's jays, and birds eat catkins and buds (Zimmerman 1991). Consumption of hazel pollen by white-footed voles, a species endemic to western Oregon and northwestern California, explained a strong association between capture rates and hazel cover (Manning et al. 2003). Oceanspray provides cover and browse for big game, and is used by dusky-footed woodrats in Oregon (Carey 1991).

Management activities that promote development and maintenance of understory vegetation can positively influence songbird diversity by maintaining habitat for shrub-associated species. Commercial thinning can favor the establishment and expansion of many shrub species, leading to the development of a vigorous understory (Tappeiner and Zasada 1993, Huffman et al. 1994). Group selection harvests in rotation age stands also can promote understory development in and adjacent to harvested patches (Chapter 2). However, modifications to conventional thinning may be required to achieve desired shrub cover, including wider spacing, uneven spacing, and protection of shrubs during harvest operations. Stand characteristics in addition to overstory cover and stem density also may affect understory vegetation. Nurse logs and decaying wood are important for the establishment of salal (Huffman et al. 1994, Huffman and Tappeiner 1997), red huckleberry (Pojar and MacKinnon 1994, Klinka et al. 1989), and western hemlock (Harmon and Franklin 1986) in forest understories. Swainson's

thrushes consumed ants and beetles that may be associated with large woody debris. Therefore, in addition to providing foraging habitat for bark-gleaning bird species, woody debris also plays a role in trophic pathways that support other songbirds. In general, managed forests have a deficit of decaying wood relative to natural forests, and the management of woody debris is a major issue in Pacific Northwest forests (Rose et al. 2001). As more information is revealed on the ecological importance of decaying wood, it is becoming apparent that current guidelines for augmenting volumes of woody debris in managed forests may be inadequate to sustain all the functions it fulfills in natural forests (Rose et al. 2001).

Although the seedlings of many shrubs establish readily following thinning, older shrubs have unique ecological values that are worth preserving. Larger, older shrubs are more likely to flower and produce seeds than smaller, younger shrubs (Harrington et al. 2002). Larger shrubs provide more vertical structure, and support more epiphytes (Rosso 2000). Forest epiphytes (lichens and bryophytes) are known to support diverse arthropod communities (Gerson and Seaward 1977, Neitlich 1993) and invertebrates inhabiting epiphytic lichens are an important food source for some birds (Pettersson et al. 1995). Thinning may increase diversity and abundance of macrolichens on shrubs, but harvesting operations that result in the loss of old shrub stems may have negative effects on some epiphytes in the short term (Rosso 2000).

Management of habitat for any one species or group of species involves tradeoffs with other species. Promoting the development of understory shrubs in managed forests is likely to enhance floristic, invertebrate, and vertebrate diversity. However, some bird species, such as golden-crowned kinglet and hermit warbler, are closely associated with conifer canopies, and others such as hermit and varied thrushes, dwell primarily in the understory of closed-canopy conifer stands (Marshall et al. 2003). Stands that are managed to develop dense understories may not provide suitable habitat for these species. To ensure habitat availability for all species, a range of forest structural conditions should be represented on the landscape.